Americardia lightbourni new species and *A. columbella* new species compared to *A. media* (Linnaeus, 1758), *A. speciosa* (A. Adams and Reeve, 1850), and the extinct *A. columba* (Heilprin, 1886) (Bivalvia: Cardiidae)

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ABSTRACT

A comparatively small and many ribbed *Americardia* living from Bermuda, off Florida to Caribbean Panama and Brazil is described and named after J.R.H. (Jack) Lightbourn. The new species has more anterior ribs and reaches a significantly smaller size than the two other Recent western Atlantic species. It also lives in deeper water, particularly in the northern part of its distribution. It is well represented in Bermuda and Brazil but has been confounded with the much larger, lower ribbed and shallow water *Americardia media*, best known from the West Indies. A comparison of the Pliocene *Americardia columba* (Heilprin, 1886) with Recent material revealed gross similarities, yet its marked distinct rib sculpture did not allow consideration of the latter material conspecific. Thus *Americardia columbella*, living from North Carolina to Yucatan, Mexico, is also described as new herein. These two new species are compared with the type species, *A. media*, living from Florida to Ascension, and its congener *A. speciosa*, living exclusively at St. Helena. Instead of one, in Florida there are three and in Brazil two, extant *Americardia*. There is only one species living in the waters of Bermuda, North Carolina, Ascension, and St. Helena, but each of these populations represents a distinct *Americardia* species. Based on the most recent studies, the application of *Americardia* is genetically, biogeographically, and morphologically supported for this Atlantic and Eastern Pacific species complex. Consequently, *Ctenocardia* is restricted to the superficially similar but spiny Indo-Pacific species-group. According to Linnaeus, 1758 and 1767, his "O[ceano] Indico" type of *Cardium medium* should be at Uppsala only. However, no type material or trace thereof could be found there. In reality, the true identity of the Linnaean species is simply unknown and conspecificity with the Indo-Pacific *Ctenocardia fornicata* could not be excluded. To stabilize one of the "best known" Caribbean cardiids a neotype from material in the Linnean Society, London is selected, and McLean's supposed type locality, Cuba, Havana is herein confirmed.

The Natural History Museum, London [NHMUK] type material of *Cardium speciosum* is comprised of four specimens, which, however, represent two species. Only one matches the original description and is confirmed as the holotype. The other three specimens were added after 1890.

Additional keywords: Western Atlantic, Bermuda, Florida, Brazil, St. Helena, *Ctenocardia*, neotype *Cardium medium* Linnaeus, 1758, *Cardium fornicatum* G.B. Sowerby II, 1840.

INTRODUCTION

In conformity with all cardiid experts, e.g. Vidal (2000: 642), and ter Poorten (2005: 6), and most regional specialists, e.g. Clench and Smith (1944), Abbott (1974: 484), and Mikkelsen and Bieler (2008: 298), Huber (2010: 300) also recognized only one large *Americardia*, living from North Carolina to Ascension, exceptionally reaching 60 mm in the Bahamas (Redfern, 2001: 226). This species was uniformly understood as highly variable, living from shallow to rather deep water and being widely distributed, including North Carolina (Porter and Houser, 1994: 19), Bermuda (Jensen and Pearce, 2009: 344), Brazil (Rios, 2009: 1479), and Ascension (Rosewater, 1975: 33).

However, Lee (2009: 33) instead recognized *Americardia columba* from NE. Florida as valid recent species and separated it from the West Indian *A. media*. Lee further mentioned some "atypical populations" of *Americardia* from Bermuda and Brazil. Subsequently, the present authors combined their respective *Americardia* holdings resulting in nearly 30 lots with over 100 specimens collected throughout the Western Atlantic. Immediately it became obvious that not only two, but in fact three, distinct Recent species from Florida were involved. These differed in the prominence of the posterior sulcus, maximum size, number of ribs, color, and notably also in biogeography and habitat. Subsequent review of material at the Florida Museum of Natural History (FLMNH, Gainesville) by the senior author revealed 27 and 28 lots respectively of the new taxa described below. In addition, he studied 12 lots of the latter new taxon in the E.F. García Collection.

Two distinct *Americardia* species were detected in a small collection of Pliocene fossils from Florida. This led to further inquiries into that fauna, including a review of the holdings at the FLMNH. Moreover, the "well known" *Americardia* having been sorted out, the identity of Ascension Island specimens was at stake inasmuch as the obscure *Cardium speciosum* A. Adams and Reeve, 1850 recognized by E.A. Smith (1890a) as living in the

S. Atlantic, is a valid congener (Huber, 2010: Chapter 5). Thus, additionally the identity and exact distribution of *A. speciosa* had to be clarified. Moreover, the NHMUK type material contained four specimens and two species, which necessitated further inquires and solutions.

Distinction from such a well known species as *Americardia media* obviously requires an unambiguous opinion on the true identity of that Linnaeus' species. Most surprisingly, this investigation led to the fact that the London material identified by Hanley (1855) cannot represent Linnaeus' true type. In Uppsala, where, according to Linnaeus (1758 and 1767), his type should be, no specimen or traces thereof could be located. Consequently, the true identity of *Cardium medium* Linnaeus, 1758 from "Oceano Indico" is simply unknown; one could not exclude it being an earlier name for the well known Indo-Pacific *Ctenocardia fornicata*. The "firm" understanding of this "well known" American species proved neither firm nor even known, but ultimately based on mere assumptions.

As a final consideration, many modern authors use instead of *Americardia*, as proposed by Stewart (1930) and recognized by Vidal (2000), the Indo-Pacific *Ctenocardia* for this group. This is also supported by the genetic analyses performed by Kirkendale (2009).

Consequently, the authors went beyond the simple question of whether indeed a second *Americardia* lives in Florida, to investigate all Atlantic species and their generic allocation, including fossil records. A neotype for *A. media* had to be designated, the holotype for *A. speciosa* had to be identified and confirmed, and two species had to be described as new to science.

All these issues are addressed below, and two species, *Americardia lightbourni* and *Americardia columbella*, are described as new to science and compared with their two Recent Atlantic congeners.

Abbreviations used in the text are: UF: Florida Museum of Natural History, Gainesville, Florida; BMAZ: Bermuda Aquarium, Museum and Zoo, Hamilton, Bermuda; NHMUK: Natural History Museum, London; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Family Cardiidae Lamarck, 1809
Subfamily Fraginae Stewart, 1930

Genus *Americardia* Stewart, 1930

Remarks: Type species by original designation is *Cardium medium* Linnaeus, 1758 as understood by "Reeve pl. 6 fig. 30". Stewart explicitly noted: "Should the identity of *Cardium medium* Linné with *C. medium* Reeve ever be questioned, the name *Americardia* is to go with the latter". Obviously, Stewart himself had noticeable doubts on the true identity of Linnaeus' species.

Linnaeus (1758: 678, 1767: 1122) gave O[ceano] Indico as type locality. However, this was changed early on by Gmelin (1791: 3247) to Oceano Americano. Subsequently, McLean (1939: 167) even specified Havana, Cuba. Neither of the latter authors saw or designated a type. Neither discussed or excluded the quite common, spined, white-purple Indo-Pacific *Ctenocardia fornicata* (G.B. Sowerby II, 1840). This species was unknown to Gmelin, but matches Linnaeus' original description precisely at least in context as sp. 61, in shape, in colors, in biogeography, and eventually even in sculpture "sulcis laevibus absque aculeis, angulisque obsoletis". Why should Linnaeus mention a not present feature within the very few words available? Is it indeed "without spines" or is it instead, "slightly angular ribs, smooth, where the spines are abraded"?

Linnaeus had no personal *Cardium medium* material but described this species without any references from the Swedish Queen Ulrike collection "M.L.U." (1758) and "M.L.U. 485 n. 34" (1767). It was not until later (Gmelin, 1791) that references leading to today's interpretation of the species were provided. Linnaeus based his species solely on a Swedish specimen, of which he apparently could find no satisfactory figure. Lister (1685: pl. 316, fig. 153) as proposed by Clench and Smith (1944: 21) was well known to Linnaeus, but not explicitly cited, so this lectotype designation is invalid. Linnaeus clearly excluded any type material in his personal collection (now in the Linnean Society, London) as he left no indication, which was his custom, with that material. Despite this, Hanley (1855: 47) isolated two unmarked valves in a box in Linnaeus' personal collection, though noting some differences. These, a right and a left valve, are illustrated online as *Cardium medium* <www. Linnean-online.org/16920> (Figures 18, 19). They conform well to specimens collected in Cuba and to the common understanding of *Americardia media* but definitely do not represent true Linnaean material contemporary with the description of *C. medium*. No doubt these specimens were introduced later, possibly by the son of Linnaeus or by the subsequent owner of the collection, Sir J.E. Smith.

Quite unfortunately, the Museum of Evolution, Uppsala University, could not deliver the requested species. E. Sjölin, Curator, wrote 19 October, 2010: "Regarding your request for photos of *Cardium medium* Linnaeus, 1758; I'm sorry to inform you that I couldn't find this specimen in the Museum of Evolution, or information of its whereabouts." Thus, one of the "best known" Western Atlantic cardiids has no type material; even the type locality and the true identity of *C. medium* are unsubstantiated.

To eliminate any doubts of the identity of *Cardium medium* Linnaeus, 1758, the unmarked right valve from the Linnean Society London, S.P. Dance label image G-M 0010260, well illustrated at <www.Linnean-online.org/16920/> is **selected as neotype** (Figure 19). McLean's (1939) assumed type locality, Havana, Cuba is supported. As such, *Cardium medium* Linnaeus, 1758 conforms, as anticipated by Stewart, to Reeve's interpretation and becomes the true type species of *Americardia*.

No solution other than that presented here would better serve taxonomic stability and the consistent interpretation of *C. medium* over the last 200 years. For some

time the Linnaean species was retained in *Cardium*; later it was transferred to *Fragum* (e.g. E.A. Smith, 1890a, b). Stewart (1930: 267) separated *Americardia* at the subgenus level from the New World *Trigoniocardia* and designated *Cardium medium* as its type. Stewart explicitly included the Panamic *Cardium biangulatum* Broderip and G.B. Sowerby I, 1829 but not the Caribbean *Cardium guppyi* Thiele, 1910 in *Americardia*. Stewart somewhat questioned his own subgeneric placement of *Americardia* under *Trigoniocardia* but clearly separated *Americardia* from the spiny sculptured Indo-Pacific *Ctenocardia* H. and A. Adams, 1857. In fact, narrow spined ribs are typical for the Indo-Pacific *Ctenocardia*, strongest expressed in the type species *Cardium hystrix* Reeve, 1844 non Lightfoot, 1786 (=*Cardium virgo* Reeve, 1845) weakest in *Ctenocardia gustavi* Vidal and Kirkendale, 2007. The western Atlantic *Americardia*-group, including the two well known Panamic *A. biangulata* (Broderip and G.B. Sowerby I 1829) and *A. planicostata* (Broderip and G.B. Sowerby I 1833) display broader and smoother ribs. In general, *Americardia* also grow larger and more solid than the usually smaller and more fragile Indo-Pacific *Ctenocardia*. Most conspicuous among the conchological differences is the ornamentation of the ribs: commarginal bars/knobs vs. spines respectively.

Vidal (2000) applied *Americardia* at generic level, distinct from the New World *Trigoniocardia*, and also separated from the Indo-Pacific *Ctenocardia*. Due to morphological affinities, however, Vidal placed both genera in the same group 2 within Fraginae. Ter Poorten (2005) and Mikkelsen and Bieler (2008) synonymized *Americardia* into *Ctenocardia* and combined the New World with the Indo-Pacific species. Lee (2009) and Huber (2010) did not follow those latter works, but applied *Americardia* to American species, generically distinct from the Indo-Pacific *Ctenocardia*.

Finally, Kirkendale (2009) genetically studied Fraginae. Her results are consistent with Stewart's and Vidal's view. *Americardia media* is in all clades more closely related to *Trigoniocardia* than *Ctenocardia*. Aside from disjunct biogeography and distinct morphology, the genetic data are consistent with the view here presented. The morphologically distinct "*Ctenocardia*" *victor* was recently recognized as unrelated *Freneixicardia* by ter Poorten (2009: 31). Pending further studies with additional *Ctenocardia* species and resolution of some inconsistent evidence of paraphyly among these generic units *Americardia* is herein treated as a valid genus within the cardiid subfamily Fraginae.

***Americardia lightbourni* new species**
(Figures 1–11, 21)

Diagnosis: Rather small and thin-shelled, deeper water *Americardia* with very numerous ribs, narrow interstices and a marked posterior sulcus.

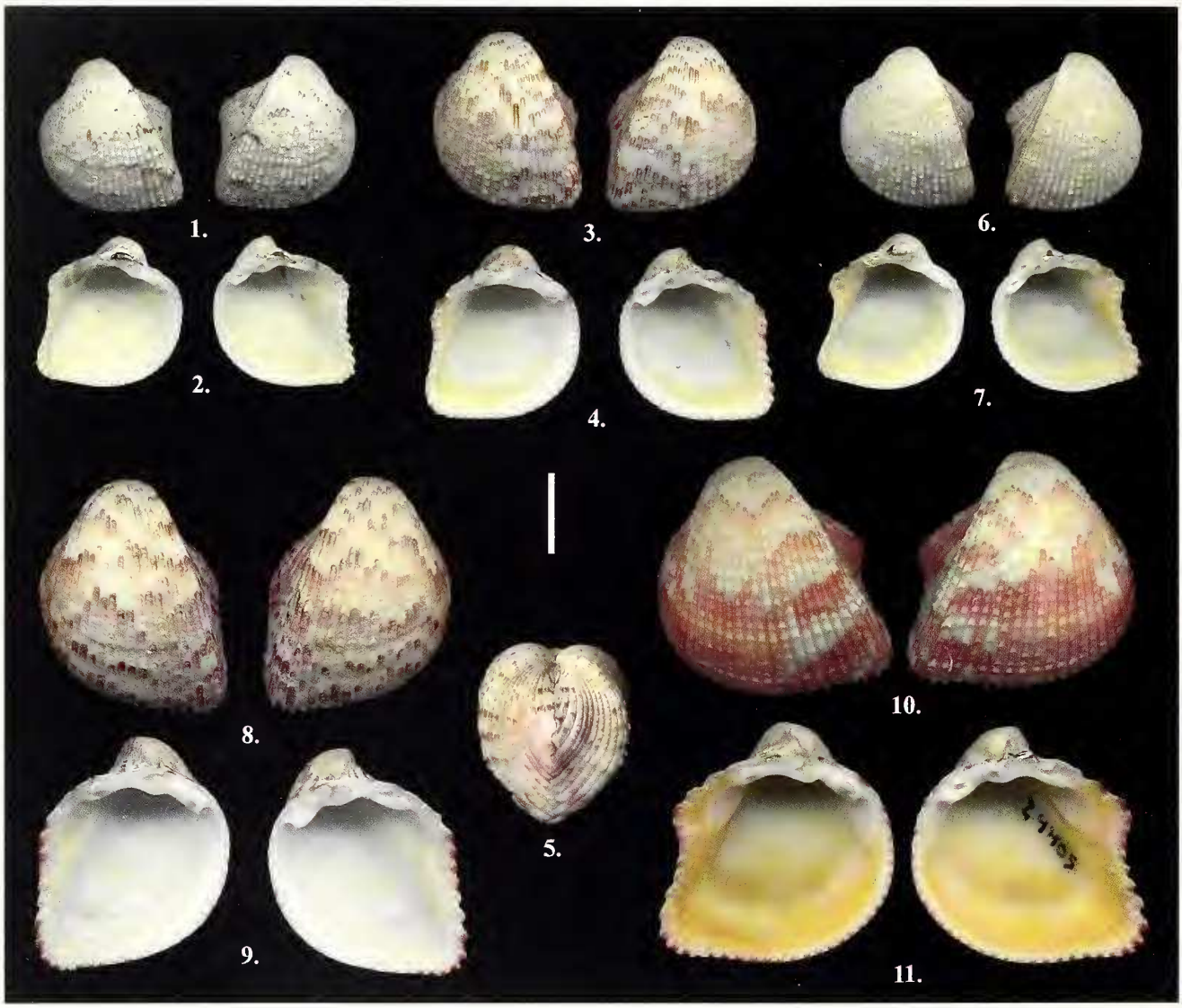
Description: Shell thin and rather fragile, inflated to strongly inflated in older specimens; moderately to strongly oblique, with a rather strong posterior sulcus. Smallest Atlantic *Americardia*, exceptionally up to 31 mm, but usually around 20 mm. Anterior margin obliquely rounded; ventral margin oblique, descending toward carina, almost imperceptibly sinuate in the posterior third. Carina sharply expressed, moderately rounded. Shell equivalve and inequilateral with rounded, weakly prosogyrous umbones placed in anterior half and extending above dorsal line. Shell surface densely radially sculptured, with 27–31, often 28 or 29, anterior ribs. Anterior ribs low, rather flat, and separated by narrow interspaces less than ¼ rib in breadth. Beneath intritacalx ribs are glossy smooth without spines, or elevated scales. Dehiscent intritacalx composed of a whitish calcareous layer, very densely and regularly commarginally lined, often forming small, irregularly arranged knobs. Ligament external, very small, dark brown, situated just posterior to umbones. External coloration whitish with irregularly arranged rose and brownish blotches and streaks. Internal shell surface porcellaneous white, usually suffused with yellow and occasionally with purplish streaks. Pallial line entire, positioned very close to the ventral margin and connecting two medium-sized, nearly homomyarian, subovate scars. Shell margin finely crenulate ventrally, but coarser on posterior margin. Hinge line strong and rather thick, with two cardinal teeth and two prominent lateral teeth. Posterior cardinal tooth in right valve and anterior lateral in left valve strong. Valves close tightly.

Variations: Size, thickness and color intensity vary remarkably within its range. Bermuda and S. Florida specimens are in general smaller with maximum sizes around 21 mm, paler and thinner, characters possibly induced by their deeper habitat. Louisiana, Caribbean Panama, and Brazilian specimens grow larger, with maximum sizes up to 32.7 mm, are often more solid, usually more brightly colored, often deep yellow inside. In the Caribbean and Brazil the species lives in much shallower water. Brazilian shells may be more elongate than the others. However, base colors and rib characters remain identical, and their habitat is still deeper than that of the type species.

Etymology: The new species name honors John (Jack) R.H. Lightbourn, who pioneered deep-water shelling in his native Bermuda and who, with the late Arthur T. Guest, discovered the holotype.

Type Locality: Bermuda Island, S. of Castle Roads, dredged in 82 m, collected by J.R.H. Lightbourn and A. T. Guest, September, 1976.

Type Material: Holotype: UF 447279, one paired specimen, 20.5 mm [Figures 1, 2], from the type locality, ex Coll. H.G. Lee. Paratype suite 1: BMAZ 2011 274 019, two paired specimens and one single right valve, 20.7 [Figures 6, 7], 20.9, and 16.3 mm respectively, from type locality, ex Coll. H.G. Lee. Paratype suite 2: Coll. M. Huber, QQ2691, one paired specimen, 25.3 mm,



Figures 1–11. *Americardia lightbourni* new species. **1–2.** Holotype Bermuda 20.5 mm. 1. External view. L, R valve. **2.** Internal view. L, R valve. **3–5.** Paratype suite 5, Brazil, 23.5 mm. **3.** External view L, R valve. **4.** Internal view, L, R valve. **5.** Posterior view, paired valves. **6–7.** Paratype suite 1, Bermuda, 20.7 mm. **6.** External view, L, R valve. **7.** Internal view L, R valve. **8–9.** Paratype suite 1, Brazil, 31.3 mm. **8.** External view, L, R valve. **9.** Internal view, L, R valve. **10–11.** Paratype suite 6, Louisiana, 32.0 mm. **10.** External view, L, R valve. **11.** Internal view L, R valve. Scale bar (all views) = 1 cm.

Caribbean Panama, off Portobello, 15 m, coral sand, dived February, 2002. Paratype suite 3: Coll. M. Huber, QQ269, one paired specimen, 21.1 mm, N. Brazil, Bahia, Alcobaça, 10–20 m, coral sand, dived March, 2005. Paratype suite 4: Coll. H.G. Lee, two paired specimens 13.1 and 15.8 mm, S. Florida, SW. Dry Tortugas, 24.736°N, 85.639°W, dredged 62.5–66.5 m, collected by E.F. García, NSF I 13. Paratype suite 5: Coll. H.G. Lee, two paired specimens, 23.5 and 31.3 mm [Figures 3, 4, 5; 8, 9 respectively], N. Brazil, Bahia, Alcobaça, 10–20 m, coral sand, dived February, 1999. Paratype suite 6: Coll. E.F. Garcia 24405, two paired specimens 21.1 and 32.0 mm [Figures 10, 11], Louisiana 28°5.85′N, 91°1.28′W, dredged 68.3 m, collected by E.F. García 3 July, 2003.

Distribution: The new species is widely distributed within the Caribbean Province, known from Bermuda, S. Florida, the Gulf of Mexico, Caribbean Panama, and Brazil. *Americardia lightbourni* is uncommon in the north but quite commonly found in Brazil.

Habitat: *Americardia lightbourni* is a sublittoral species, living from 10–100 m depth. In the southern part of its range, it is found in shallower water, 10–70 m, whereas in the north it is usually found at 50–100 m. The substrates are sand, coral-sand, and mixed carbonate rubble (off Louisiana). It is of relevance that in all collections studied the type species, *A. media,* is limited to much shallower habitats.

Discussion and Comparison: *Americardia lightbourni* can be separated from *A. media* by its higher rib number, and consequently by finer internal shell surface crenulation. The interstices are narrower, the posterior sulcus is stronger, and the valves are in general thinner and more fragile. In addition, *A. lightbourni* reaches only half the size of *A. media*. Whereas *A. media* is a common, shallow water species, often found beached, *A. lightbourni* is deeper dwelling, especially in the northern part of its distribution, and is less frequently found. The distribution of *A. lightbourni* surpasses the known range of *A. media*, which does not reach Bermuda or central Brazil.

Similarly, the new species is separated from *A. columbella* new species by its greater number of anterior ribs and a much finer crenulation of the internal margin. In addition, the area adjacent to the posterior sulcus is flat, not sunken as characteristic of *A. columbella*. The sulcus here is less marked compared to the very strong expression in *A. columbella*. *Americardia lightbourni* is more oblique compared to the rather square, upright shape of *A. columbella*. *Americardia lightbourni* is also markedly smaller and less solid than that species. Their distribution is close in Florida; otherwise *A. lightbourni* is much more widely distributed. Both species live in the sublittoral although in the northern part of its distribution *A. lightbourni* dwells in deeper water, living in general below 50 m, whereas *A. columbella* is most often found from 20 to 40 m.

From the Pliocene of Florida (e.g., APAC Pit, Sarasota) there is an apparently unnamed *Americardia* sp. (Figure 24), which has a comparable number of about 29 ribs and similar outline and surface features. Compared to Recent material, the valves of this fossil taxon are more compressed. Additionally, it is less oblique, the intercostal areas are broader, the beaks are lower and more posterior (central), and the posterior angulation is weaker. The senior author found this taxon in about ten percent of the approximately 200 Plio-Pleistocene *Americardia* lots housed at the UF collection. About half of these (approximately 10) lots also contained *A. columba*, and the two seemed to be morphologically distinct without overlap. Specimens were present in material from the Bermont, Caloosahatchee, Late Duplin, and Tamiami formations. Interestingly, only one lot referable to *A. media* was encountered [UF 35360 USA: Florida: Charlotte Co., Punta Gorda Quad, Tamiami Formation, Pinecrest Beds R. Portell! 12/23/88]. This station produced several other unusual taxa (R. Portell, pers. comm., 21 Dec., 2010). Nonetheless this extinct *Americardia* sp., apparently coeval with *A. columba* (Figure 23), may well represent the ancestor of *A. lightbourni*.

Cardium speciosum A. Adams and Reeve, 1850 was described from China in the notorious Samarang Report (see Huber, 2010: 75). As with nearly half of the bivalves newly described therein, *C. speciosum* was never again collected in Chinese waters. E.A. Smith (1890a: 302) recognized its misallocation, compared it with Atlantic specimens, and accepted it as a St. Helena species, likely collected on the return "voyage" from China.

The type material is difficult to analyze. NHMUK 74.12.11.392 represents a specimen, undoubtedly from St. Helena and labeled type. This "type" specimen is accompanied by three specimens labeled "syntypes". Thus, the whole lot contains four specimens, which, however, represent two distinct species. Originally, Adams and Reeve did not give any size or indicate more than one specimen. Furthermore, E.A. Smith (1890a: 302) only referred to "the type of this species preserved in the British Museum." Adams and Reeve clearly indicated 26 ribs. None of the present four specimens has 26 ribs. All of the three "syntypes" have far in excess of 30, up to 35 ribs. Together with shape and color, these three "syntypes" can be dismissed as subsequently introduced *A. media,* neither originating from the original lot nor St. Helena. The "type" itself has 28 ribs, two thereof admittedly rather weak. Otherwise it matches the original description well with its strongly oblique shape, moderately marked sulcus, solid texture, presence of reddish marks, and commarginally sculptured interstices. It is here recognized as the holotype (Figure 20). Consequently, the other NHMUK "syntypes" should be removed from the type collection.

In the general collection there is an unambiguous lot, NHMUK 1889.10.1.1960-4, comprised of five well preserved specimens collected in the 19th Century by Lt. W.H. Turton at St. Helena. These, together with recently collected specimens, allowed us to finally characterize *A. speciosa* as expressed herein. The exact depth of occurrence is still unknown, but it is presumed to be sublittoral.

Another lot, NHMUK 1889.10.9.38, collected by Conry at Ascension Is., is of importance. These shells confirm E.A. Smith's (1890b: 322) identification: they match *A. media* in having 25–26 anterior ribs, a solid shell, a rather broad and weakly sulcate shape, and the same color pattern. This record confirms the southernmost occurrence of this species.

In many respects *A. speciosa* and *A. lightbourni* represent extremes of this small Atlantic *Americardia*-group. *A. lightbourni* has the highest rib count; *A. speciosa* has the lowest; *A. lightbourni* is rather fragile, whereas *A. speciosa* is solid. Their maximal sizes differ markedly, and their distribution is disjunct.

Americardia columbella new species
(Figures 12–17, 22)

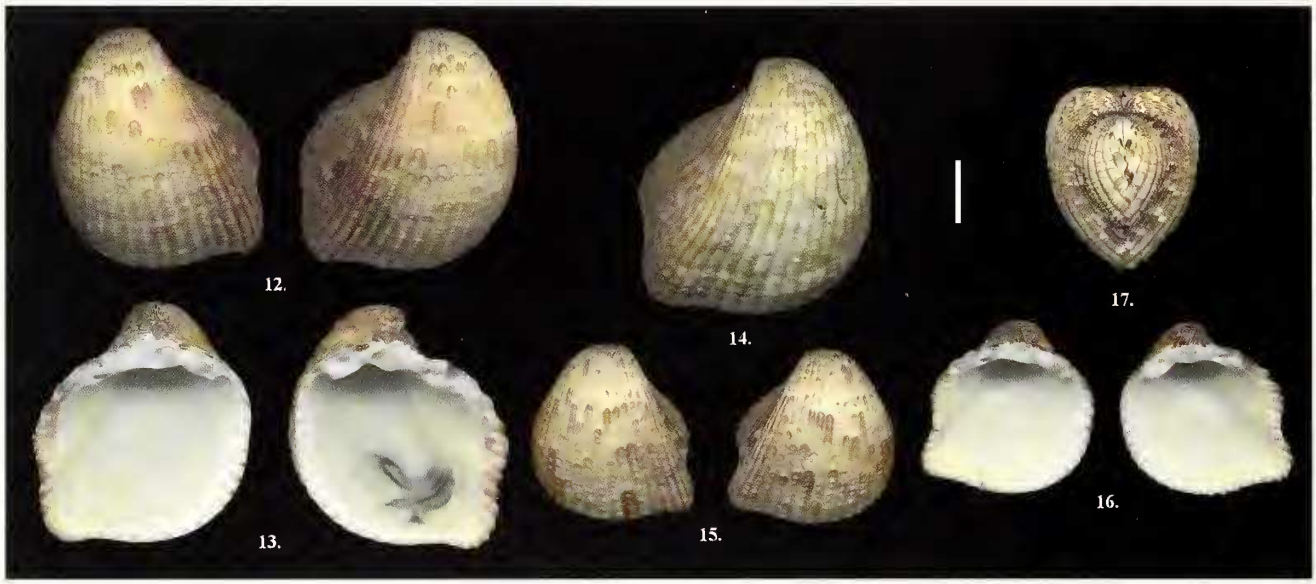
Americardia media "Linnaeus" Porter and Houser (1994: 19, North Carolina) *non* Linnaeus, 1758.

Americardia columba "Heilprin" Lee (2009: 33, pl. 7, sp. 119, NE. Florida) *non* Heilprin, 1886.

Americardia media "Linnaeus" Huber (2010: 300 fig. 11, left specimen, NE. Florida) *non* Linnaeus, 1758.

Americardia media "Linnaeus" Tunnell et al. (2010: 353, Texas) *non* Linnaeus, 1758.

Diagnosis: Large, quadrangular, orange-brown *Americardia* with distinct posterior sulcus and intermediate number of ribs, closely adjacent and without any interstices anteriorly.



Figures 12–17. *Americardia columbella* new species. **12–13.** Holotype, NE Florida, 42.2 mm **12.** External view L, R valve. **13.** Internal view L, R valve. **14.** Paratype suite 1, NE Florida, 44.5 mm. External view, R valve. **15–17.** Paratype suite 1, NE Florida, 30.1 mm. **15.** External view L, R valve. **16.** Internal view L, R valve. **17.** Posterior view, paired valves. Scale bar (all views) = 1 cm.

Description: Shell solid and thick, large for genus, reaching 44.5 mm in NE Florida, inflated to strongly inflated in old specimens; subquadrate, with a strong posterior sulcus, which is strongest extended medially. Anterior margin evenly rounded; ventral margin nearly straight, weakly sinuate in posterior third. Posterior angulation marked but moderately rounded. Shells equivalve and subequilateral, with rounded, orthogyrous umbones nearly centrally placed and clearly extending above the dorsal line. Surface radially sculptured, with 23–25, usually with 24 anterior ribs. Anterior ribs touching each other, eliminating any flat interspace as found in all other *Americardia*. Ribs subtrigonal in cross-section, with highest elevation in posterior third. Ribs beneath intritacalx glossy, smooth, without spines or elevated scales. Dehiscent intritacalx composed of orange-brown calcareous layer, very densely and regularly commarginally lined, often forming small knobs on highest part of ribs. External ligament very small, light brownish, situated just posterior to umbones. External coloration whitish with irregularly arranged orange-brown blotches and streaks. Overall shell appears brownish-orange. Internal shell surface in general glossy-white, brown along posterior margin. Pallial line entire, positioned close to ventral margin and connecting two mediums-sized, nearly homomyarian, subovate scars. Margin strongly crenulate. Crenulations broader centrally and narrower on both sides. Hinge line strong and rather thick with two cardinal teeth and two prominent lateral teeth. Posterior cardinal in right valve and anterior lateral in left valve strong. Valves close tightly.

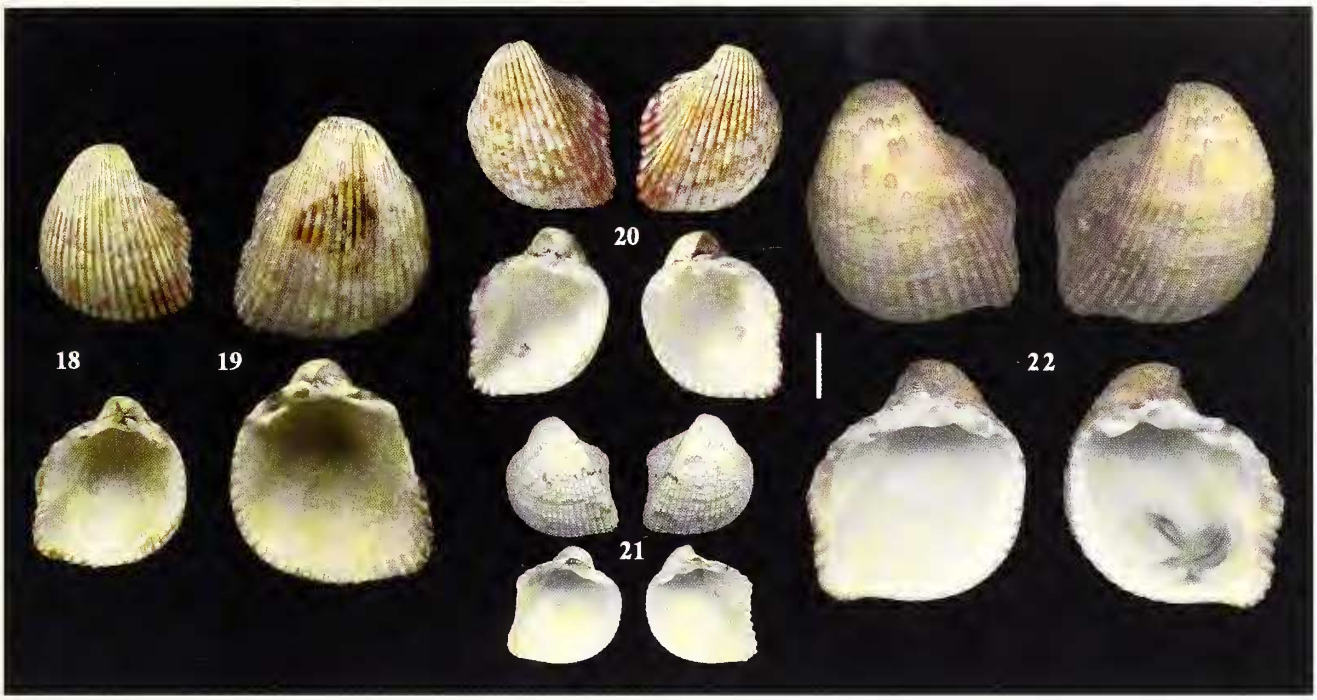
Variations: Externally, rarely a weak purplish-red band is present, in addition to the typical orange-brown blotches; inside, occasionally purplish spots or streaks are found; rarely the 3–4 ribs immediately anterior to the carina may be separated by very narrow interstices; invariably, however, the anterior portion never has interstices. In general, southern and western Florida specimens are smaller, lighter colored, and occur in deeper water.

Etymology: This new *Americardia* is named as diminutive of *columba* (from the extinct *A. columba.)* The Pliocene Florida fossil shares morphological features with and may represent the ancestor of *A. columbella.*

Type Locality: Eastern USA, NE Florida, St. Johns Co., Nine Mile Reef, 9 miles ESE St. Augustine, 22 m, near reef, on sand; 1 September, 1979, H.G. Lee (dive).

Type Material: Holotype: UF 447280, one paired specimen, 42.2 mm [Figures 12. 13], from the type locality, ex Coll. H.G. Lee. Paratype suite 1: USNM 1156949, one single valve, 44.5 mm [Figure 14], and three paired specimens, 9.9 to 30.1 mm [Figures 15, 16, 17], from the type locality, ex Coll. H.G. Lee. Paratype suite 2: Coll. M. Huber, QQ232, two paired specimens, NE. Florida, 60 miles SSE St. Augustine, dredged in 40 – 43 m, June, 1978; larger specimen, 29.2 mm illustrated in Huber (2010: 300 fig. 11, left specimen). Paratype suite 3: Coll. H.G. Lee, five paired specimens, 15.5 to 38.5 mm, same data as holotype. Paratype 4: Coll. H.G. Lee, one paired specimen, 30.6 mm; NE. Florida, Mayport, dredged in 21.5 m, November, 2009.

Distribution: This new species is narrowly restricted geographically, only known from the southeast coast of North America, from North Carolina to Yucatan. It is

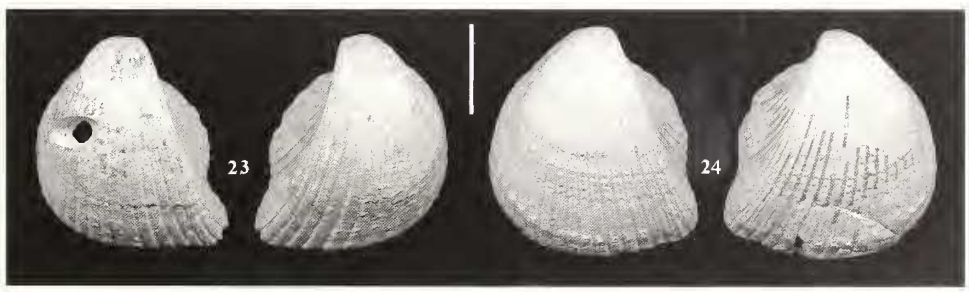


Figures 18–22. Western Atlantic *Americardia* species. **18.** *Cardium medium* Linnaeus, 1758, 29 mm, Linnean Society Collection. **19.** *Cardium medium*, neotype, Linnean Society Collection 16920 [online] (Dance image G-M 0010260), 37 mm. **20.** *Cardium speciosum* A. Adams and Reeve, 1850, holotype, NHMUK 74.12.11.392, 28.5 mm. **21.** *Americardia lightbourni*, holotype, 20.5 mm. **22.** *Americardia columbella*, holotype, 42.2 mm. Scale bar (all views) = 1 cm.

rather uncommonly encountered and rarely, if ever, cast ashore (personal observations; Andrews, 1971, 1992; Odé, 1973, 1975; Rice and Kornicker, 1962; Vokes and Vokes, 1984; UF 328133 H.E. Vokes!).

Habitat: *Americardia columbella* lives sublittorally offshore, with many records from 20–40 m, occasionally down to 60 m; the substrates vary from shell grit to coarse and fine siliceous sands, rarely on carbonate bottoms. It is of relevance that, in all collections studied, the type species, *A. media*, is restricted to much shallower habitats.

Discussion and Comparison: With the type species, *Amerieardia eolumbella* shares a comparatively large size, a solid shell, but also a broad hinge and an identical dentition. The rib count is comparable, although *A. media* often has one or two more anterior ribs. The carina in *A. columbella* is generally more prominent, weaker, and more rounded in *A. media*. The shape is more quadrangular upright, whereas *A. media* shape is more oblique anteriorly. *Amerieardia eolumbella* is most easily separated by its more prominent posterior sulcus and its more vivid orange red color. Moreover, the area adjacent to the sulcus is typically sunken in *columbella*, whereas in *A. media* this area is flat. Unmistakably distinct is the rib sculpture; *A. media* has rather flat-topped ribs with rather broad interstices, but the interstices are completely missing in *A. eolumbella*, and the ribs are subtrigonal in cross-section. The two



Figures 23–24. *Americardia* fossil species. **23.** *Americardia columba*, Pliocene, Florida, external view L, R valve. **24.** *Americardia* sp., Pliocene, Florida, external view L, R valve. Scale bar (all views) = 1 cm.

differ in geographic distribution: *A. media* is mainly a West Indian species, occasionally found in southern Florida and southeastern Mexico, and *A. columbella* is not known outside of eastern North America, in the Carolinian portion of the Caribbean Province. *Americardia media* lives just subtidally and is commonly beached, whereas *A. columbella* is a sublittoral species, rarely, if ever, cast ashore. The common *A. media* and the rather uncommon *A. columbella* are often found in sizes between 25–30 mm; however, the maximum size of *A. media* is 61.3 mm (West Indies, NHMUK, while *A. columbella* is not known to exceed 44.5 mm (paratype 1). *Hemicardium columba* Heilprin (1886: 93) was described as a Pliocene Floridian fossil from two left valves, illustrated on his pl. 11 figs. 26 and 26a, up to 20 mm. Heilprin compared it to the Recent *Hemicardium medium* of southern Florida. He noted 23 anterior ribs and additionally 13 on the posterior slope. Compared to *H. medium*, Heilprin noted that *H. columba* "its more upright form, the deeper hollowing of the posterior face, and the more pronounced carination of the umbonal slope". In this regard *A. columba* neatly shares the features found in the Recent *A. columbella*.

However, well preserved Pliocene fossils from Florida revealed a character not mentioned by Heilprin, namely a very distinct rib sculpture (Figure 23). In *Americardia columba*, the comparatively broad ribs are low and rather flat, separated by a deep flat channel. Thus the rib structure of *A. columba* closely approaches that of *A. media* while it is quite different from *A. columbella* with its lack of interstices and higher, subtrigonal ribs. Moreover, the Recent material is broader in shape and clearly sinuate at the margin of the valves posterior third. The original coloring of the extinct species is unknown. Due to similarities in shell shape, it is hypothesized that *A. columbella* is a comparatively young species derived from an old Floridian stock represented by *A. columba*.

Cardium speciosum is only known from St. Helena, and *A. columbella* only from the southeast coast of North America. If the locality is known, these two cannot

Table 1. Comparison of the four Recent Atlantic *Americardia* species.

	A. media	*A. lightbourni*	*A. columbella*	*A. speciosa*
anterior ribs	24–27, often 25	27–31, often 28 or 29	23–25, often 24	21–23, often 22
anterior rib sculpture	Rather flat and broad; interstices about 1/3 rib breadth	Low and narrow, rather flat, interstices less then 1/4 rib breadth	Elevated, subtrigonal, higher posteriorly, adjacent and no interstices	Subtrigonal, higher posteriorly, interstices about 1/2 rib breadth
posterior sulcus	Weakly expressed sulcus, flat adjacent area	Marked sulcus, flat adjacent area	Strongly marked sulcus, moderately to strongly hollowed adjacent area	Marked sulcus, flat adjacent area
shape	Usually moderately higher than long, weakly oblique, carina weakly expressed	Narrow (Brazil) to broadly oblique, carina sharply expressed	Quadrate, upright, carina sharply expressed	Narrow and strongly oblique, carina broadly rounded
size	61.3 mm [West Indies, NHMUK], often above 40 mm in the West Indies, but smaller in the north and in the south	Exceptionally 32.7 mm (Gulf of Mexico); 31.3 mm (Brazil), but usually smaller, not known above 21 mm in FL and Bermuda	44.5 mm (N.E. Florida), often above 30 mm in the north, smaller in the southern part of Florida	38.6 mm [NHMUK]
color	Rather uniform externally, white with brownish blotches; internally white, often marked with brownish blotches or streaks	Variable, whitish with orange, rose, and brown streaks, internally white suffused with yellow, more intensely colored in Gulf of Mexico and the south	Rather uniform, externally white with numerous orange and darker brownish blotches, internally porcelaneous white, less intensely colored in S. Florida	Rather uniform, white with numerous orange, reddish or rose blotches, internally yellowish-white, rose-red on the posterior margin
distribution	S. Florida, Bahamas, S.E. Mexico, Roatan, Puerto Rico, Venezuela, Grenada, N. Brazil, Ascension; common in the West Indies	Bermuda, S.E. Florida, Gulf of Mexico, Caribbean Panama-Central Brazil; rather common in Brazil	North Carolina to Mexico; found along entire Florida coast but uncommon in the very S., Texas, Yucatan	restricted to St. Helena
habitat	Subtidal, usually 1–13 m, up to 23 m; often beached	Sublittoral 10 – 100 m, deeper north (50–100 m), shallower south (10–70 m)	Sublittoral, 20–40 m, down to 60 m; rarely beached	unknown, presumably sublittoral

be confused. They possess a similar exterior color, reach similar sizes, and both have solid shells. However, typically their shape is markedly distinct: narrow and oblique, with a moderately expressed sulcus in *A. speciosa* and broad, subquadrangular, with a prominent sulcus in *A. columbella*. *A. speciosa* has a significantly lower rib count, with interstices of about half a rib's breadth, while in *A. columbella* the number of anterior ribs is greater, and interstices are lacking. Internally, *A. speciosa* is yellowish, even deep yellow in some specimens; *A. columbella* is glossy white within.

CONCLUSIONS

The simple question, whether the "Recent" Floridian *A. columba* is indeed distinct from "*A. media*" led to many unexpected results. Identification of material from various locations proved straightforward, with one exception. Smaller south Florida material was difficult. The cause of this predicament appears to be threefold: firstly, three species may be found there, secondly, cardiids globally develop many of their taxonomic characteristics only at medium to large size, and third, it could not be completely excluded that some specimens represent hybrids. The authors are convinced that instead of one, three species of *Americardia* live in Florida waters. A fourth Atlantic species evolved in St. Helena. Evidence suggests that a second undescribed and now extinct *Americardia* lived coevally with the well known Pliocene *A. columba* in Florida waters. Based on the diversity encountered in this study, it is suggested that *Americardia* originated in, and radiated from, this area.

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